Chapter 4
Earthworm Life Histories and Biology

4.1 Life Cycles

Our knowledge of the life cycles of even quite common species of temperate and tropical species of earthworms is still very inadequate, and there are many species about which we know very little of their life cycles. This situation is not improving since the type of normal history studies that involve observations of basic biology of organisms such as earthworms is not made naturalists as they were in the nineteenth and early twentieth century. Hence, a lot of our information on earthworm life histories goes back to these periods.

Earthworms breed continuously or intermittently once they have reached sexual maturity under suitable environmental conditions (Olive et al., 1978). The ova of earthworms are contained in cocoons (oothecae), which differ in shape with species, and which most lumbricids deposit close to the soil surface. The cocoons of some common lumbricids are illustrated in Fig. 4.1. If the soil is very moist, earthworms will deposit their cocoons near the surface, but placing them much deeper in the soil when it is dry or cold. Cocoons can be produced at any time in the year, but most species of earthworms produce their cocoons when the temperature, soil moisture, food supplies, and other environmental factors are most suitable. However, there is good evidence that peak cocoon production occurs in the spring or early summer in the northern hemisphere. It has been demonstrated clearly in cultures (Evans & Guild, 1948) and in the field (Gerard, 1967) that seasonal fluctuations in the soil climate can cause the number of cocoons produced by different species of earthworm to vary considerably from year to year.

Since cocoons are produced from the clitellum, the size of a cocoon is probably correlated with the size of the earthworm. Lavelle (1981) plotted cocoon size against fresh weights of adults for 11 European lumbricid species and tropical species of several families and reported a strong positive correlation between size and weight of cocoons and bodies.

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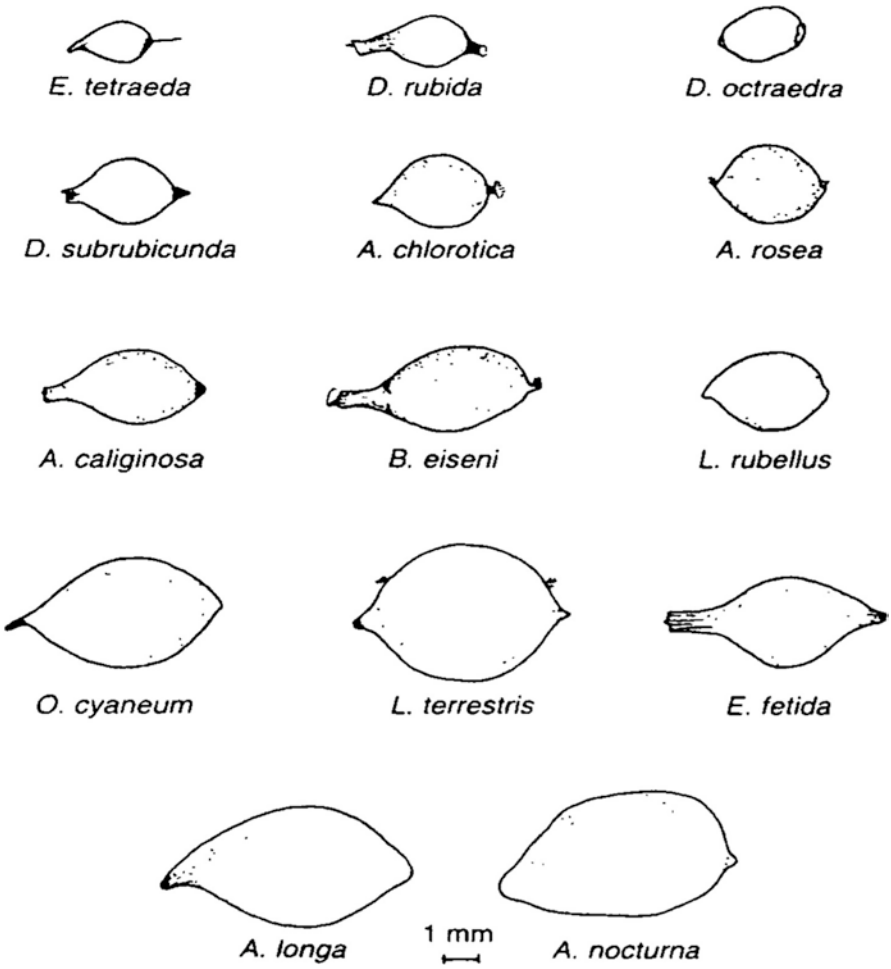

Fig. 4.1 Cocoons of common lumbricids (from various sources)

Evans and Guild (1948)) reported that, in cultures of common species of lumbricids, in the United Kingdom, for a year, at optimum soil moisture, the numbers of cocoons produced by each species paralleled closely seasonal changes in soil temperature (Fig. 4.2). Fewest cocoons were produced in the winter months, and there was a temperature threshold of about 3 °C, below which few or no cocoons were produced. Many cocoons were produced from the end of February to July when temperatures were rising, and the greatest numbers of cocoons were produced between May and July. Thereafter, the numbers of cocoons produced decreased quite rapidly as temperatures fell, particularly for some lumbricid species. Gerard (1967) confirmed these conclusions by sampling in the field for the cocoons of *Aporrectodea caliginosa* and *Allolobophora chlorotica*. In his study, most cocoons occurred in soil samples collected in May and June. Probably, more cocoons were

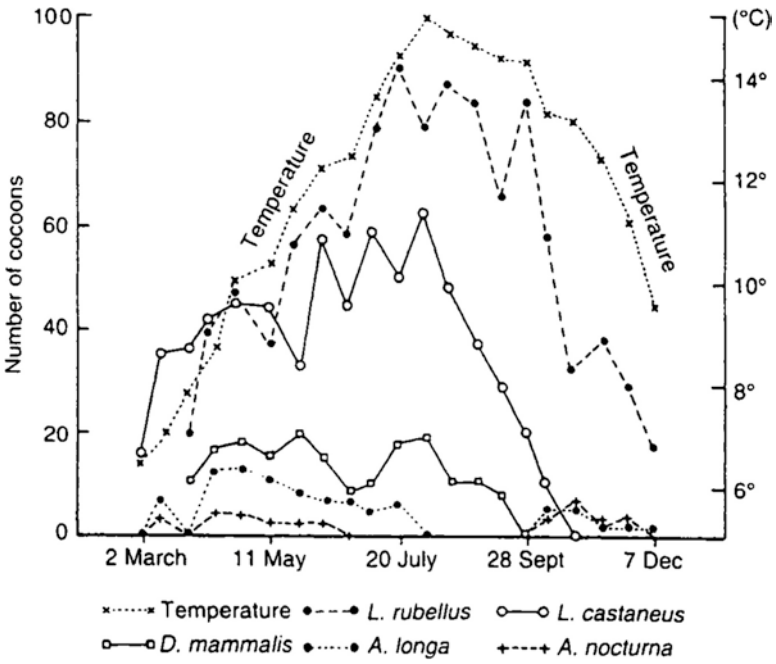

Fig. 4.2 Seasonal production of cocoons of temperate lumbricids

produced in July and later, but by this time the cocoons would be hatching faster than they were being produced, so the overall numbers found in soil samples would decrease. Very few cocoons occurred in soil samples taken from August to November. Although some cocoons were found in the December, January, and February samples, these had probably accumulated over time, because cocoons produced during the colder months would not normally hatch until the soil warmed up in the spring.

Some species of lumbricids, such as *Aporrectodea longa* and *Allolobophora nocturna*, pass through an obligatory diapause during the summer months and hence produce cocoons only from mid-March to June or early July and October to November. Other lumbricids belonging to species of the genera *Eisenia* and *Octolasion* and other species of *Allolobophora* species may have a facultative diapause during dry periods, and this also interrupts the production of cocoons.

The number of cocoons produced in a season per individual earthworm differs greatly with both species and climate (Evans & Guild, 1948). In one study, between 3 and 79 cocoons were produced by individuals of 8 different earthworm species in culture (von Wilcke, 1952). In another investigation, *A. caliginosa*, *A. longa*, and *O. cyaneum* produced between 3 and 13 cocoons per year. *Allolobophora chlorotica* produced 25–27 and *L. rubellus*, *L. castaneus*, and *Dendrodrilus rubidus* 42–106 cocoons per year (Satchell, 1967). Edwards (1988) reported that *Dendrobaena veneta* could produce 84 cocoons per year; *Eudrilus eugeniae*, 188; *E. fetida*, 198;

and *Perionyx excavatus*, 1014. Phillipson and Bolton (1977) reported that *A. rosea* produced only 3–4 cocoons per year, but Nowak (1975) found that Polish earthworms produced between 26 and 42 cocoons per year.

Satchell (1967) pointed out that there was a direct correlation between the numbers of cocoons produced by any earthworm species and how much this species was exposed to adverse environmental factors such as desiccation, extremes of temperature, and predation. In other words, those species of earthworms that may be exposed regularly to harsh environmental hazards normally tend to produce more cocoons to enable them to survive adverse conditions. Thus, those earthworm species that live in, or can move into, the deeper soil layers where they are protected from adverse conditions, e.g., *L terrestris*, *A. longa*, and *O. cyaneum*, produce fewest cocoons, whereas those species that live near the surface, such as *L. castaneus*, *L. rubellus*, and *Dendrobaena subrubicunda*, which are exposed more directly to such factors, produce very many more. *Lumbricus castaneus* survives summer droughts in western Europe mainly as eggs protected in cocoons, i.e., it avoids climatic stress by surviving as an inactive stage (Wallwork, 1983). Because individuals of any species of earthworm are influenced mainly by the prevailing environmental conditions, they produce fewer cocoons not only when the soil is too dry but also when it is too wet (Evans & Guild, 1948). Since cocoons can resist desiccation and cold, they probably enable earthworm populations to survive adverse conditions. Another factor that can influence the numbers of cocoons produced by earthworms is the state of nutrition of the adults that produce them; for instance, earthworms fed on materials such as sewage sludge, straw, or farmyard manure produced fewer than one-tenth of the cocoons that were produced by earthworms fed on bullock or horse droppings, or peat.

In the semiarid steppe grassland of Russia, *Eisenia nordenskioldi* was reported to restrict cocoon production to the period of the summer rains (Pokarzhevskii & Titisheva, 1982). In the southern hemisphere, cocoon production is also seasonal, as Madge (1969) showed for African eudrilids. In India, cocoon production is related to the monsoons, with maximum cocoon production occurring in late October and early November (Dash & Senapati, 1982). *Millsonia anomala* in the Ivory Coast in Africa can produce cocoons at any time in the year, but there are two peaks of cocoon production which coincide with soil drying at the end of the wet season, resulting in two distinct generations per year (Blanchart et al., 1993). In South Australia, the largest populations of the introduced lumbricid species *A. trapezoides* and *A. caliginosa* occurred from winter to early spring in five pastures (Baker et al., 1992). Adults were restricted to winter and spring, when breeding occurred. Subadults and juveniles, but few adults, survived the summer.

The time that cocoons take to hatch varies considerably among species, ranging from 3 weeks for *Bimastos zeteki* (Murchie, 1960) to 5 months for *Eisenia rosea* (von Wilcke, 1952). The overall time earthworms take to reach sexual maturity from hatching differs greatly between species and has been investigated in detail for only a few species, and mostly in culture. Temperature also affects the time for development before the cocoons hatch. For instance, Gerard (1967) found that cocoons of *A. chlorotica* hatched after 36 days at 20 °C, 50 days at 15 °C, and 112 days at 10 °C. Table 4.1 provides some data on the periods of growth of some species kept

Table 4.1 Time to maturity in weeks of several earthworm species

Month when growth began	*Allolobophora caliginosa*	*Allolobophora chlorotica*	*Allolobophora longa*	*Dendrobaena subrubicunda*	*Allolobophora rosea*	*Eisenia fetida*	*Lumbricus castaneus*	*Lumbricus rubellus*
November 1944	–	42	–	–	–	74	–	–
December	–	39	38	–	–	–	–	–
January 1945	–	35	–	33	–	70	–	–
February	–	30	–	29	–	74	–	–
March	–	29	–	27	–	–	–	–
April	58	–	71	27	–	–	–	–
May	53	–	70	22	62	–	–	–
June	56	–	64	–	61	–	–	–
July	54	–	58	–	53	47	18	37
August	–	–	54	–	50	–	–	–
September	–	–	51	–	–	–	–	–
February 1946	–	–	40	42	–	–	–	–
March	–	–	–	38	–	–	25	–
April	–	–	–	33	–	–	25	–
May	–	–	–	32	–	–	25	–

in culture (Evans & Guild, 1948). Edwards (1988) reported that the time that cocoons of *E. fetida* took to hatch was 32–73 days; *E. eugeniae*, 13–27 days; *P. excavatus*, 16–21 days; and *D. veneta*, 40–126 days but varied with temperature. Michon (1954) showed that the type of food available also influenced the length of the maturation period. The incubation times of cocoons of *Pheretima hilgendorfi* can range from 244 to 264 days, which is considerably longer than that of most other lumbricid species. Clearly, the production and time for maturation of cocoons differ with species, population density, age structure, available food, moisture, and temperature.

The life span of mature lumbricids in the field is probably often no more than a few months (Satchell, 1967), because they are exposed to many hazards such as predation, although their potential longevity is 4–8 years (Lakhani & Satchell, 1970). In a field site, Satchell (1967) reported that *L. terrestris* matured in 1 year but that environmental factors affected the time taken for growth to maturity greatly. *Allolobophora chlorotica* took from 29 to 42 weeks to mature at field temperatures, those earthworms that matured during the winter months taking longest, but Gerard (1967) calculated that *A. chlorotica*, hatching in a field site in late July, took only 21 weeks to mature. Graff (1953) recorded that *A. chlorotica* took 17–19 weeks to mature when kept at 15 °C, and Michon (1954) reported that the same species matured in 13 weeks at 18 °C. In protected culture conditions, individuals of *A. longa* have been kept for more than 10 years, *E. fetida* for 4½ years, and *L. terrestris* for 6 years, although in the field they are unlikely to attain such ages. Longer times to reach maturity must be expected if soil conditions are poor. Michon (1954) studied the life span of other species and reported that they ranged from 15 months for *A. chlorotica* to 31 months for *A. longa*, in a group of ten species kept at 18 °C, with an average life span for all species of 2 years. Data for the times of development of some lumbricid earthworms were given by von Wilcke (1952) (Table 4.2). Earthworms stop breeding some time before they die. For *D. subrubicunda*, the

Table 4.2 Time of development for some lumbricid worms

Species	No. of cocoons per worm per year	Incubation time of cocoon (weeks)	Period of growth of worm (weeks)	Total time for development (weeks)
E. fetida	11	11	55	66
D. subrubicunda	42	8½	30	38½
L. rubellus	106	16	37	53
L. castaneus	65	14	24	38
E. rosea				
(A. rosea)	8	17½	55	72½
A. caliginosa	27	19	55	74
A. chlorotica	27	12½	36	48½
A. terrestris				
F. longa (A. longa)	8	10	50	60

active breeding period, which is when the clitellum is prominent, is only half the total adult life span, i.e., 100–350 days out of a total of 550–600 days (Michon, 1954).

The life cycles of only a few species from other families of earthworms have been studied in any detail, but they probably differ from those of lumbricids mainly in time of development. Although *Pheretima* spp. can produce cocoons throughout the year in culture, in the subtropical climate of India, most cocoons were produced from March to June, and relatively few during the rainy months of July and August. In Japan, cocoons of *Pheretima hupeiensis* hatched mainly in May; immature earthworms grew rapidly but hibernated in both the immature and mature stages (Watanabe, 1975). The length of earthworms can range from less than a centimeter to 2 m for some tropical species. The dimensions of British lumbricids range from 2 to 30 cm (Arthur, 1965) (Fig. 4.3).

The life cycles of earthworms, in families other than the Lumbricidae, were studied by Lavelle (1974, 1978). The numbers and time of cocoon production, growth, and longevity did not differ significantly from those of lumbricid earthworms, other than that relatively fewer cocoons were produced overall (Table 4.3). Rates of cocoon production and growth were correlated with both temperature and moisture.

The life cycle of *P. hupeiensis* has been studied in North America (Grant, 1956). Mature earthworms occurred from June to October. Young earthworms first appeared in July and reached largest numbers in September, immatures probably overwintering as immatures. All the available evidence was that *P. hupeiensis* has an annual life cycle, in the United States with most of the mature individuals dying soon after reproduction occurs. Lavelle (1971) studied the life cycle of the acanthodrilid, *Millsonia anomala* in West Africa in detail. Cocoons hatched during the wet seasons after 18–30 days of incubation. The young earthworms took 10–14 months to mature, and they may not have lived much longer than this, because survival over dry seasons was mainly as immature stages. A typical structure of a population pyramid in July was 1.7% over 24 months old, 67% between 16 and 19 months old, 18.3% between 11 and 12 months old, 48.30% between 6 and 8 months old, and 25% between 1 and 2 months old.

Madge (1969) studied the life history of a eudrilid species in Nigeria. He concluded that the first generation of *Hyperiodrilus africanus* was produced during the dry season and that these developed into mature individuals during the second dry season and produced cocoons at the beginning of the next wet season, to produce a second generation per annum.

Fully clitellate individuals of the acanthodrilid worm *Diplocardia egglestoni* occurred only during May and June in an area of Michigan, USA, during a dry summer (Murchie, 1958). Similarly, clitellate adults of *Bimastos zeteki* were found from May to mid-July. The cocoons of this species were abundant in late May and June, and some were found in late summer. There seemed to be evidence of considerable numbers of this species overwintering as immatures (Murchie, 1960). The breeding period of the marsh-dwelling worm *Criodrilus lacuum* (Glossoscolecidae) was restricted to about 2 months, from the end of April to the end of June, and such a short breeding period may be common among marsh-dwelling oligochaetes. *Alma* spp., a microchaetid earthworm from Egypt, lives in the mud of ditches and

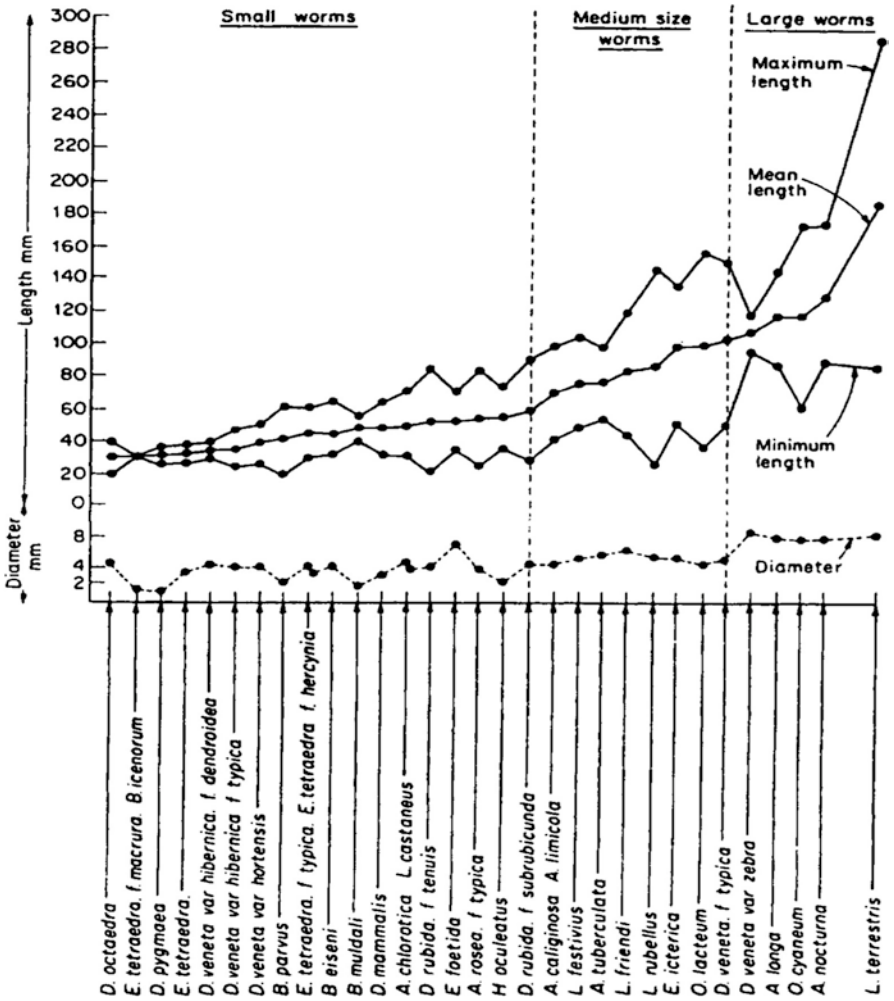

Fig. 4.3 The dimensions of British lumbricids. (Modified from Arthur, 1965)

produces cocoons before the mud dries up during the hot season; this enables it to survive adverse conditions. Little is known of other aspects of the life cycles of these less-studied families.

Hamoui (1991) reported that *Pontoscolex corethrurus* (Mueller) from Brazil took 14–19 months after hatching, before cocoons were produced, and thereafter, cocoons were produced for a further 12–16 months. Murchie (1960) reported that individuals of the species *B. zeteki* do not become sexually active for 12–24 months after hatching or, if they emerged at the beginning of a dry period, this might take as long as 22–26 months. Obviously, the growth periods of different species of earthworms differ greatly and can vary considerably for any given species depending on environmental conditions.

Table 4.3 Life cycle of nonlumbricid species of earthworms from a tropical habitat (Lavelle, 1979)

Species	No. of cocoons produced annually	Time for growth (months)	Maximum longevity (years)
Dichogaster agilis	7.5–15.8	15	2–2.5
Chuniodrilus zielae	5.9	18	1.5–2.0
Millsonia anomala	5.6–14.2	20	2.0–2.5
Millsonia lamtoiana	2.4–2.8	24	2.0–3.0
Agastrodrilus opisthogynus	0.4–1.9	24	3.0–4.0
Dichogaster terrae-nigrae	1.3–2.4	36	4.0
Millsonia ghanensis	0.8–1.4	42	4.0–5.0

4.2 Earthworm Reproduction

4.2.1 Spermatogenesis

Earthworms are hermaphrodites with separate testes and ovaries that function simultaneously in the same individual. Groups of spermatogonia are formed from follicles (masses of reproductive cells) in the testes and pass into the seminal vesicles; these contain male cells at all stages of development. These cells eventually form spermatozoa which, at first, float freely in the seminal vesicles but pass quickly into the testis sacs and attach themselves to the surface of the sperm funnels, where they remain until copulation occurs. During mating, they are swept by the cilia of the funnel into the vas efferens and then to the exterior through the male pore via the vas deferens so they reach the ova externally.

4.2.2 Oogenesis

The first stage of the development of the ova normally occurs in the basal part of the ovaries, with the formation of oogonia, which divide and form oocytes. These do not divide again but increase in size and accumulate yolk. The oocytes are shed from the ovaries into the ovisacs, where reduction division takes place, by the rupture of the peritoneum. When ripe, the ova are discharged from the oviducts through the female pores and pass into the future cocoon which is secreted by the clitellum. However, the ova of eudrilid earthworms are transferred to the ovisacs at a much earlier stage of development, so that their ovaries are much smaller, except during the very early stages of sexual development.

4.2.3 Copulation and Fertilization

Most earthworm species reproduce by cross-fertilization, although a number of species can also produce cocoons parthenogenetically. *Lumbricus terrestris* mates on the soil surface, but many other species mate in soil belowground. Many species mate periodically throughout the year, except when environmental conditions are unsuitable or when they are estivating or in diapause.

Methods of copulation are not identical for all species. When individuals of *L. terrestris* mate, two earthworms, which are attracted to each other by glandular secretions, lie with the ventral parts of their bodies together, and their heads pointing in opposite directions (Fig. 4.4). They come into close contact in the region of the spermathecal openings where the clitellar region of one earthworm touches the surface of the other. While copulating, the earthworms do not respond readily to external stimuli such as touch and light. Large quantities of mucus are secreted so that each earthworm becomes covered with a slime tube between segment 9 and the posterior border of the clitellum, the two slime tubes adhering to, but remaining independent of, each other.

A seminal groove (normally seen only as a pigmented line) extends from the male pore to the clitellum, but this groove may not be very obvious in some species. Each seminal groove is a depression of the outer body wall formed as a series of pits by the contraction of muscles, the arciform muscles, which lie in the longitudinal muscle layer. These muscles do not contract simultaneously but successively, beginning at segment 15, each contraction forming a pit. These pits carry seminal fluid as droplets from the male pore to the clitellar region, where it collects and eventually enters the spermathecae of the mating earthworm. Individuals of *Eisenia fetida* have been seen to clasp and release each other several times, and such movements may assist the entry of the sperm into the spermathecae. Tembe and Dubash (1961) described the copulation of a species of *Pheretima* that has three or four pairs of spermathecae. The male pores first come into contact with the hindmost pair of spermathecal apertures and discharge seminal fluid and prostatic fluid into them. Each earthworm then moves backward, and the seminal fluid is discharged into the next pair of spermathecae, until all have been "charged." Different methods of sperm transference have been observed in other species; for instance, the octochaetid earthworm *Eutyphoeus waltoni* has spermathecal openings and male pores on raised papillae. The latter, termed penes, are inserted into the spermathecal openings. The eudrilid earthworm species, *Schubotziella dunguensis* has a single median male pore formed from two fused copulatory pouches, and a single median spermatheca; during copulation, the two pouches (which communicate with the male ducts) evert and are inserted into the opening of the spermathecae. All these species that transfer the spermatozoa by direct methods do not form mucous tubes as do lumbricids.

A number of earthworm species transfer the sperm cells between individuals in spermatophores, ensuring that the ova are fertilized as they are produced. The production of spermatophores may be facultative or obligate (Bouché, 1975). Spermatophores were first observed in *Bimastos antiquus michalisi*, from Albania,

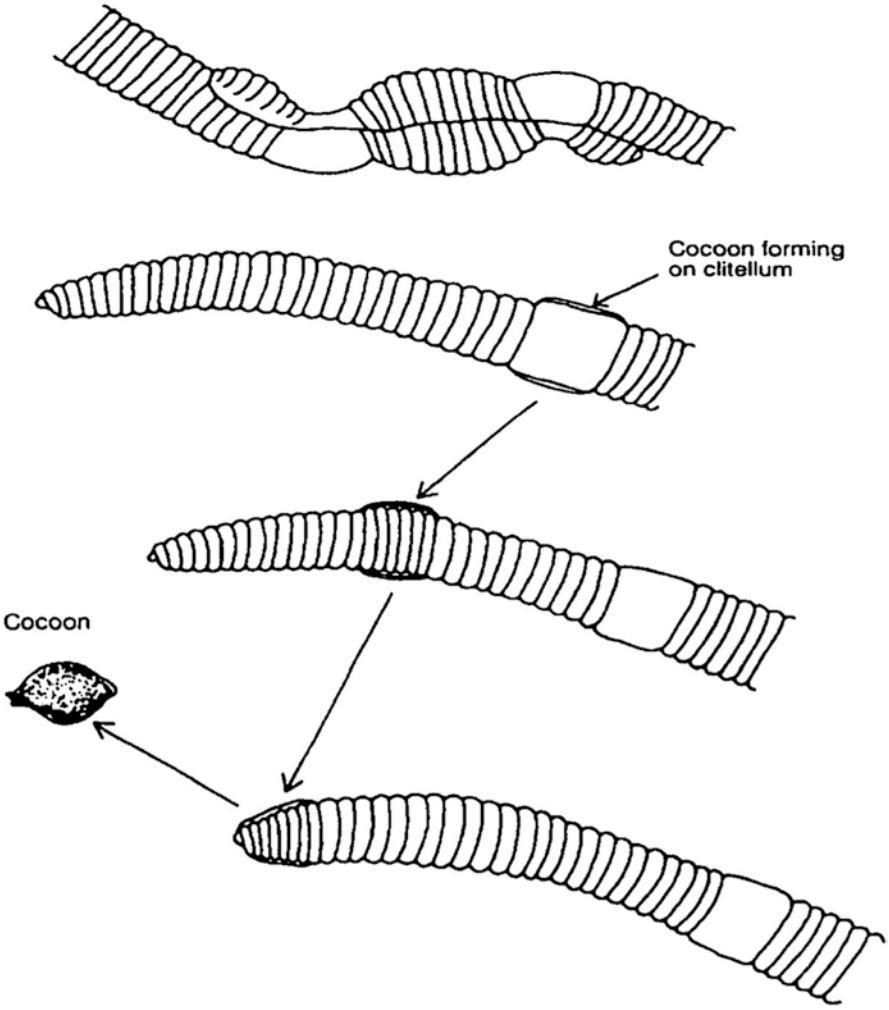

Fig. 4.4 Copulation and stages in cocoon production in Lumbricidae. (Tembe & Dubash, 1961)

but have been reported for more than 20 species of earthworms from the genera *Aporrectodea*, *Bimastos*, *Dendrobaena*, *Dendrodrilus*, *Eisenia*, *Eisenoides*, *Kritodrilus*, *Lumbricus*, *Murchieona*, *Octolasion*, and *Satchellius*.

Some eudrilid worms are unusual in that they seem to have a mechanism for internal fertilization. Sims (1964b) described the fertilization of a *Hyperiodrilus* sp. where fertilization is internal in a special chamber (the bursa propulsoria) that is connected to both the spermathecal system and the ovisac.

Copulating earthworms have to keep close together, and the contours of the ventral surfaces at the points of closest contact help to achieve this. Some setae in segments 6–10 are shorter, thicker, and less curved than normal. They flex inward and

grip the partner, and the long, pointed, and grooved setae on the ventral surface of the clitellar region pierce the body wall of the opposing earthworm. After copulation, which may take as long as an hour, the earthworms separate, and each clitellum produces a secretion which eventually hardens over its outer surface. When this is hard, the earthworm moves backward, so drawing the tube over its head, and when the earthworm is completely free, the ends of the tube close, to form the cocoon, which is roughly lemon-shaped, but with a shape typical of each species (Fig. 4.1). The cocoon contains a nutritive albuminous fluid, produced by the clitellar gland cells, the ova and the spermatozoa which were discharged into it as the tube passed the spermathecal openings. Cocoons continue to be formed until all the stored seminal fluid has been used up. Fertilization of eggs, which occurs in the cocoon, is external.

The cocoon wall consists of interwoven fibrils, which are soft when first formed, but later become much harder and very resistant to drying and damage. The ends of cocoons are extended into processes or tufts which may be stem-like, conical, or umbrella-like, according to species. Cocoons vary in color from whitish (when formed) to yellow, greenish or brownish, and differ greatly in size (Fig. 4.1). The very large Australian earthworm, *Megascolides australis*, probably produces the largest cocoons, which may measure up to 75 × 20 mm. However, the size of the earthworm does not always correlate with the size of the cocoon; for example, *L. terrestris* produces cocoons measuring about 6.0 × 4.5–5.0 mm, whereas species of *Pheretima*, which are about the same size as *L. terrestris*, produce much smaller cocoons, about 1.8–2.4 × 1.5–2.0 mm.

The number of fertilized ova in each cocoon ranges from 1 to 20 for most species of lumbricid earthworms but usually only 1 or 2 survive and hatch. Out of 14 species of lumbricid earthworms tested in culture, it was reported that *E. fetida* was the only species that commonly produced more than one earthworm from a cocoon, averaging 3.3 hatchlings per cocoon (Evans & Guild, 1948; Edwards, 1988). In a detailed study of the hatching of cocoons of *E. fetida* and *Bimastos tumidus* (Vail, 1974), some of these variabilities were elucidated. Of 250 *E. fetida* cocoons, 21.5% did not hatch; 14.7% produced one young; 25.0% produced two young; 21.5%, three young; 14.1%, four young; 2.0%, five young; and 1.2%, six young. Of those that hatched, the average number of young earthworms was between two and six.

In other studies, the hatching of 100 *B. tumidus* cocoons was studied; of these, 19 failed to hatch; 6 produced 1 young earthworms; 17, 2 young; 28, 3 young; 24, 4 young; 3, 5 young; and 3, 6 young; with an average number of young per cocoon of 3.11 (Vail, 1974). Edwards (1988) reported that cocoons of *Eudrilus eugeniae* produced an average of 2.3 hatchlings per cocoon.

Some species can reproduce parthenogenetically. *Aporrectodea*, *Allolobophora*, and *Lumbricus* species can breed only sexually, but *Dendrobaena* species can sometimes be parthenogenetic and *Octolasion* spp., *Eiseniella* spp., *Aporrectodea rosea*, and *Dendrobaena rubida f. tenuis* are usually parthenogenetic (Satchell, 1967) and *E. fetida* facultatively parthenogenetic. The male organs of *A. rosea* are sterile, so that the production of all cocoons must be parthenogenetic. Asexual reproduction by fragmentation and regeneration does not seem to occur at a significant level in

terrestrial earthworms. Parthenogenesis is sometimes considered to be associated with the absence or regression of secondary sexual organs (spermathecae and prostates).

4.2.4 Parthenogenesis

Most megadrile earthworms reproduce by normal cross-fertilization, and parthenogenesis was considered to be associated with some form of parasitism. However, beginning with the work of Gavrilov (1939, 1960) and Muldal (1952b), parthenogenesis has begun to be accepted as a relatively widespread phenomenon in earthworm reproduction. Muldal (1952b) stated that there was no reason to believe that cross-breeding is obligatory and parthenogenesis rare on the basis of chromosomal studies of lumbricids. Other workers have reported various forms of parthenogenesis to occur in a wide range of species (Kobayashi, 1937; Gavrilov, 1939; Reynolds, 1974; Gates, 1974), although not all of these have been confirmed and may have been overemphasized.

Reynolds (1974) discussed the phenomenon at length, and he defined 35 North American species as having sexual reproduction (amphimictic), 11 as probably having sexual reproduction, 4 as usually having sexual reproduction but with facultative parthenogenesis, 1 as having possibly parthenogenetic reproduction, and 30 as having mainly parthenogenetic reproduction. Some workers consider these to be overestimates of the extent of parthenogenesis. Other species that have been described as having parthenogenetic reproduction include *Microscolex dubius*, *Plutellus papillifer*, *P. umbellulariae*, *Pontodrilus bermudensis*, *Udeina avesicula* (Ljungström & Reinecke, 1969), *Pontoscolex corethrurus* (Ljungström, 1970), *Pheretima alexandri*, *P. anomala*, *P. campanulata*, *P. dejecta*, *P. elongata*, *P. exigua*, *P. glabra*, *P. hilgendorfi*, *P. meridiana*, *P. rimosa*, *P. virgo*, *P. infantilis*, *P. varians*, *P. voeltzkowi*, *P. zoysiae* (Gates, 1960, 1961), *Eukerria hortensis*, *E. subandina* (Gavrilov, 1960, 1967), *Malabaria levis*, and *M. sulcata* (Gates, 1966). However, some workers have questioned whether it has been fully established through experimental evidence that many of these species do have mainly parthenogenetic reproduction.

Probably one of the more important indicators of parthenogenesis is evidence of male sterility, and this includes retention of testes and seminal vesicles in a juvenile state in adults and absence of iridescence of the male funnels, ducts, and spermathecae, which demonstrates the aggregation of mature sperm. A lack of externally adhesive spermatophores is not a good indication of parthenogenesis, because they have been found even in obligatory parthenogenetic species of lumbricids.

Reproduction cannot occur without a clitellum, ovaries, oviducts, and possibly the ovisacs, but the male organs are not essential, so the absence in various degrees of testes, seminal vesicles, seminal receptacles, vas deferens, copulatory chambers, penes, prostates, spermathecae, tubercula pubertatis, and genital and penial setae may be indications of either occasional or obligatory parthenogenesis.

Evans and Guild (1948) investigated whether some lumbricid earthworms could produce viable cocoons without mating and fertilization, by rearing individuals of 19 species in isolated cultures. In general, *Allolobophora* spp. produced no cocoons even though they were observed for periods of up to a year. Individuals of *L. castaneus* and *L. rubellus* began producing cocoons 5–6 months after they became mature, but those of *L. rubellus* were not fertile, and out of a total of 1704 cocoons produced by *L. castaneus*, only 3 produced young earthworms. The other two *Lumbricus* species produced some cocoons, but none were viable. Some individuals of the other species tested produced cocoons at different intervals after they became sexually mature. Most individuals of *D. rubida* and *D. subrubicunda* produced viable cocoons soon after they became mature, but a few individuals of the latter species did not produce cocoons for 9 months. Most unmated earthworms of the species *E. fetida* produced cocoons within 9 months of maturity, although in the same period mated earthworms produced more cocoons. Only one individual of *Octolasion cyaneum* and one of *O. lacteum* produced any viable cocoons. The same authors cross-mated individuals of *L. rubellus* and *L. festivus*, which are closely related species and similar in size. An average of five to six cocoons were produced by each earthworm, and 3 months after mating, hybrid worms emerged from some of the cocoons.

4.2.5 Polyploidy

In the Lumbricidae, about half of the karyotypes that have been investigated are polyploid. In the other families of this group, the data are few and discontinuous, but it is clear that hermaphroditism is not a precondition for the occurrence of polyploidy; in fact, another condition seems to be necessary to ensure evolutionary success of the polyploid emerging races, i.e., parthenogenesis. When polyploidy is closely associated with parthenogenesis, it results in an unexpected amount of heterozygosity which is advantageous for the individuals, conferring on them high resistance to environmental stresses.

Many authors have demonstrated that potentially parthenogenetic polyploid earthworm populations tend to have a much wider geographical distribution, but it is difficult to say if this is a result of parthenogenesis or polyploidy. Asexual reproduction confers a biological advantage, since a single thelytokous individual can easily colonize any area to which it is introduced. An important question is the elucidation of the ecological relations between the different karyological strains within the same species. Can they coexist in the same area or does the polyploid replace the diploid race? There are reports supportive of both hypotheses. Undoubtedly, better knowledge of the autoecology of the different karyological races is needed to clarify this question.

4.3 Quiescence, Diapause, and Estivation

At some times in the year, the soil close to the surface may become too dry, too cold, or too warm for earthworms to survive in it. Earthworms have several ways of surviving such adverse periods. For instance, cocoons can resist desiccation and extreme temperatures much better than adult earthworms, and the cocoons hatch when soil conditions become more favorable. Alternatively, earthworms may migrate to deeper soil where the moisture and temperature conditions are better. For instance, Madge (1969) observed that two species of eudrilid worms in tropical Africa moved down into deeper soil layers during the dry season. *Lumbricus terrestris* and *A. longa* can move readily to deeper soil through their more or less permanent vertical burrow system. Many species of earthworms that normally live near the surface move from the top layers of the soil and become comparatively inactive in deeper soil during adverse periods. Three states of such inactivity can be distinguished:

1. *Quiescence*: In which the earthworm responds directly to adverse conditions, particularly drought and high temperatures and becomes active again as soon as conditions become favorable. Bouché (1972) distinguished two types of quiescence: (a) anhydrobiosis, a response to dehydrative aggregates and loss of water, and (b) hibernation, a response to low soil temperatures. Earthworms are coiled in small cells below the frozen layers.
2. *Facultative diapause*: Which is also caused by adverse environmental conditions but does not terminate until a certain critical time after conditions become favorable.
3. *Obligatory diapause*: Which occurs at a certain time or times each year, independent of current environmental conditions but usually in response to a certain sequence of environmental changes or to some internal mechanism. These stimuli are usually such that adverse conditions tend to occur during the period of diapause.

The term “estivation” has been used to cover any or all of these states, but it applies properly only to the passing of summer or dry seasons in a dormant state. In the temperate zones, earthworms usually become quiescent during very warm spells. Many immature earthworms of the species *A. chlorotica*, *A. caliginosa*, and *A. rosea* become quiescent when the soil is either too dry or too cold (Evans & Guild, 1947), but more earthworms become quiescent during the summer than during the winter, probably because earthworms can tolerate wet and cold conditions better than hot and dry ones (Gerard, 1967). The difference between quiescence and facultative diapause is probably only one of degree. Gerard (1967) thought that quiescent behavior enabled earthworms to exist for long periods on their reserves, when there was little food available in their environment. Lee (1951) stated that in many pasture soils in New Zealand that are subject to severe drought in summer, earthworms move to deeper soil layers and become quiescent. Murchie (1956) reported that *D. egglestoni* can enter a period of quiescence or facultative diapause

in response to drought or low soil temperatures. It has been claimed that red-pigmented earthworms, which include many species of the lumbricid genera *Lumbricus* and *Dendrobaena*, do not go into diapause (Michon, 1957), but there is some evidence that *L. terrestris* does go into facultative diapause.

At the beginning of diapause, earthworms stop feeding, empty their guts, and construct a small round or oval cell lined with mucus. Then they roll into a tight ball, the body often forming one or two knots in the process, with the two ends of the earthworm tucked into the center of the ball. The coiled shape and the mucus-lined cell reduce water loss to a minimum.

Aporrectodea longa (Morgan & Winters, 1991) and *A. nocturna* have been reported to go into obligatory diapause (Satchell, 1967), as have *L. festivus*, *L. rubellus*, and some species of *Eophila*. These species, which begin to go into estivation as early as May, lose all secondary sexual characters such as the clitellum during diapause and usually come out of diapause spontaneously in September or October. By contrast, *A. caliginosa*, *A. chlorotica*, and members of the genera *Eisenia* and *Octolasion* probably undergo facultative diapause. Morgan and Winters (1991) reported that they considered that *A. longa* had an obligatory diapause in the summer from May to August/September. Prior to diapause, this species acquired energy stores in the form of lipids, and they discussed the ecophysiological significance of these changes. Byzova (1977) considered that for *A. caliginosa*, glycogen reserves are stored in chloragogenous tissues before diapause but that this can be used up in 2 months, thereby limiting the potential time of diapause. Michon (1954) stated that these species do not diapause if they are kept at 9 °C and are given adequate amounts of food, but other work by Doeksen and van Wingerden (1964) has not confirmed this. Doeksen and van Wingerden (1964) considered that diapause in lumbricids was induced by substances excreted by the earthworms themselves. On the basis of laboratory experiments, they concluded that during the active period, the concentration of these substances increases until the earthworms eventually enter diapause, after which excretion of these substances decreases. From the available evidence, it seems likely that the differences recorded between obligatory diapause, facultative diapause, and quiescence in European lumbricids represent a continuous gradation in response among species, dependent upon the severity of the environmental stresses imposed upon them (Lee, 1985).

4.4 Earthworm Growth

It was considered that earthworms continue to grow throughout their lives by continually adding segments proliferated from a "growing zone" just in front of the anus (Hyman, 1940). However, Sun and Pratt (1931) reported that earthworms emerged from the cocoon possessing the full adult number of segments and grew by enlargement of segments, although Gates (1949) challenged these findings. Moment (1953a, b), studying *E. fetida* in culture, stated that newly emerged earthworms possessed, on average, the same number of segments as adults, and the only

earthworms that grew by adding segments were those dissected from cocoons. He also observed individual earthworms from the time that they emerged from the egg and noted that although they increased in size many times, the number of segments always remained the same. Probably the correct conclusion as to the way earthworms grow was given by Evans (1946), who stated that most species possess the adult number of segments on hatching, whereas a few species add further segments during postemergence growth. Supporting this conclusion, Vail (1974) reported that the young of *E. fetida* possessed between 22 and 28 distinct segments and those of *Bimastos tumidus* 69–128 distinct segments. The higher numbers are the same as those reported for adults. However, some species of *Lumbricus* have fewer segments as they get older, even though they continue to increase in size.

Young earthworms tend to be colorless on hatching, with their circulatory system showing through the cuticle due to the presence of hemoglobin in the blood. They vary very considerably in length, and in cocoons with several young, there is a tendency for the longest earthworms to emerge first. The earthworms continue to grow, and, except for changes in pigmentation, there are few external morphological changes until maturity is reached (Vail, 1974). All the evidence is that the numbers of segments change little during growth for *E. fetida*, and for *B. zeteki* (Murchie, 1960) except when there is autotomy and regeneration (Moment, 1953a, b).

The growth pattern of *A. caliginosa* in field cultures was studied by Nowak (1975). From a mean live weight of 27 mg at hatching, the earthworms grew to a mean live weight of 325 mg after 20 months. There was a rapid prereproductive phase of growth followed by a phase of steadily decreasing growth after sexual maturity was attained. Similar results following a sigmoid growth curve were reported by Phillipson and Bolton (1977) for *A. rosea*. Many workers have confirmed such a sigmoid growth curve for *E. fetida* and other species that grow in organic wastes in processing them into vermicomposts (Edwards & Neuhauser, 1988); Edwards et al., 2010).

Lumbricus terrestris bred in culture under field conditions continued to increase in weight for about 3 years (Satchell, 1967). The increases in weight each year occurred almost entirely during autumn and spring, whereas during the winter and summer months, little weight was gained, and some was even lost. After 3 years, the average weight of the earthworms began to decrease, possibly because some weight may be lost before death.

Michon (1954) studied the development and growth of *D. subrubicunda* in culture at two temperatures. He reported that individuals gained weight rapidly until they reached sexual maturity, but after this, there was a much slower increase in weight, until the disappearance of the clitellum indicated the onset of senescence. During this last period, there was a slow decline in weight until the eventual death of the earthworms. Murchie (1960) studied field populations of *B. zeteki* and reported that the time taken for individuals to reach full body size depended on the time of year that they emerged from the cocoons. Individuals that emerged in autumn and overwintered as small earthworms and those that emerged in the spring grew rapidly, achieving full size by August, and became reproductive the following spring, i.e., within a period of 12–24 months. Those earthworms that emerged

during the summer months, at the beginning of a dry period, grew less rapidly and could take 22–26 months to reach maturity.

The population of an earthworm species at any one time is made up of young immature, well-grown immature (adolescent), mature, and senescent individuals, the relative proportions depending on the time of year (Fig. 4.5). The numbers of earthworms in the first three of these categories, for the species *A. nocturna* and *A. caliginosa*, were studied in samples taken over a period of 9 months from August to May. At the beginning of September, the population consisted mainly of immature and adolescent worms, but this was followed by a rapid increase in the number of sexually mature earthworms of both species. The numbers of adolescent earthworms remained low throughout the rest of the period, with only a small increase in numbers of *A. caliginosa* in spring, although the numbers of adolescent *A. nocturna* increased considerably at this time of year. The maximum longevity of earthworms in the field is poorly understood. *Eisenia fetida*, *L. terrestris*, and *A. longa* have been kept alive in cultures for 4.5, 6.0, and 10.2 years, respectively, but it seems likely that survival is for 2 years or less in the field. In tropical conditions in West Africa, *M. anomala* populations attained sexual maturity after 8–14 months and growth continued for a further 20–21 months (Fragoso & Lavelle, 1992). Pollution from neonicotinoid insecticides and heavy metals has the potential to inhibit growth as well as damage DNA and cause oxidative stress (Yan et al., 2021).

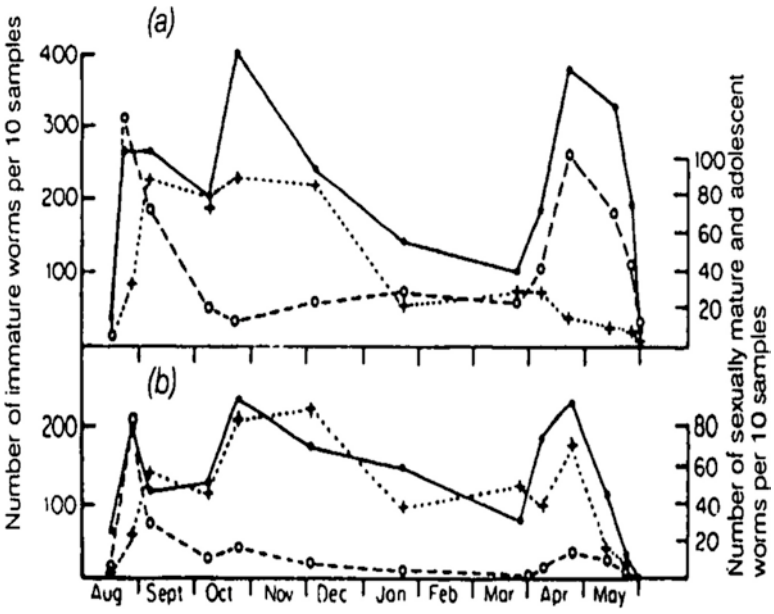

Fig. 4.5 Seasonal trends in populations of immature (•), adolescent (o) and sexually mature (+) earthworms: (**a**) *A. nocturna*; (**b**) *A. caliginosa*

4.5 Behavior Patterns

Many aspects of earthworm behavior are discussed further in Chap. 5, but there are important behavioral patterns that are not mentioned elsewhere in this book. For instance, all earthworms are very sensitive to touch, the pattern, and speed of their reaction differing between both the species and circumstances. A good example is the behavior of *L. terrestris* when it scavenges for food on the soil surface. While doing this, it usually keeps its tail in its burrow, but if it comes into contact with an object such as a stone, it will usually stop and move forward around the object. If the earthworm is touched, it withdraws back into its burrow, sometimes very quickly, and does not emerge again for some time. However, this withdrawal reaction is usually much less violent if the earthworm is almost completely in its burrow when touched, when it withdraws from the immediate vicinity of the stimulus only. If an earthworm is grasped while partly out of its burrow, it will actively resist any attempt to pull it completely out, by extending its posterior setae into the burrow wall and expanding its posterior segments, so as to grip the walls of the burrow and completely fill its exit. It is then very difficult to pull the earthworm from its burrow particularly if it is a large individual, and often it will break in two rather than relinquish its grip. After an earthworm has been subjected to such very violent treatment, it may become "alarmed" and retreat deeply into its burrow, often remaining there for a long period. The nervous mechanism of this escape behavior was analyzed by Pallas and Drewes (1981). This behavior is particularly noticeable when the formalin method of sampling for *L. terrestris* is used. If an attempt is made to remove an earthworm, which has come to the soil surface under the stimulus of the formalin, before it is clear of its burrow and the earthworm is allowed to escape, it does not usually emerge again, even when more formalin is poured into the burrow.

Many other kinds of stimuli applied to the soil promote activity in earthworms and cause them to come to the soil surface; these include vibrations caused by a fork inserted into the soil, stamping on the soil surface; indeed birds often peck hard at stones on the soil surface to induce earthworms to emerge from their burrows. Earthworms also respond to electrical stimuli applied to the soil. A wide range of chemicals including formalin, potassium, permanganate, soap solution, or mustard solution when applied to soil will bring earthworms to the soil surface.

Many species react vigorously to tactile stimuli; for instance, Murchie (1960) reported that individuals of *B. zeteki* and *E. fetida* reacted to touch in three different ways. If pricked sharply or handled, they produce a series of lashing movements from side to side, their bodies forming U-shapes with each movement. Certain species of *Pheretima* and *Eudrilus* also do this. Individuals of *B. zeteki* often eject coelomic fluid from the dorsal pores when touched, and other earthworm species can eject this fluid to a considerable height (Section 1.7). The third and least common response is autotomy, or breaking off posterior segments. Either grasping or impaling the rear end of an earthworm may cause it to break at a point a little in front of the stimulated region, and such a break can occur at any point up to 32

segments from the posterior end. Stimuli applied to the anterior end do not cause reaction in the same way.

It has been claimed that autotomy is an indication of senescence, but this is certainly, not always so for *B. zeteki* which will shed posterior segments whether young or old. Evidence that autotomy was common in this species was given by Murchie (1960), who reported that many field-collected earthworms tended to have fewer segments than reared ones. Thus, there is little evidence of posterior regeneration in this species. *Diplocardia mississippiensis* seems to undergo autotomy readily even in healthy earthworms. Where this occurs spontaneously, the front one-quarter to one-third of the body, consisting of 40 or more segments, breaks off (Vail, 1972).

4.5.1 Feeding Behavior

Individuals of *L. terrestris* feed on decaying leaf and other plant material obtained from the soil surface. They do not feed to any great extent on the leaf material in situ, but first pull it into the mouth of the burrow, to a depth of 25–75 cm, so forming a plug which may protrude from the burrow. There have been several suggestions as to why they do this. It may be in order to camouflage the entrance to the burrow, although the plug often makes the burrow more obvious. Alternatively, it may be to prevent the entry of water into the burrow during heavy rain or to keep out cold air. Whatever the reason, these earthworms never leave the mouths of their burrows exposed and will replug them very quickly if the original plug is removed. If the mouth of the burrow is in an area where there is insufficient organic material to form a plug, they will use inorganic material, commonly small piles of stones, termed middens or cairns, which may be seen in gravel paths, blocking the mouths of burrows. Individuals of *L. terrestris* normally consume food material mainly within their burrows, and since far more material is stored than can be used between normal foragings, there is adequate food when inclement conditions on the soil surface prevent them from foraging, or when the local food supply is temporarily exhausted.

Lumbricus terrestris selects its food material carefully and pulls many kinds of leaves into the burrows by the tip of the laminae, leaving the nonpalatable petioles or stems projecting from the burrow. Darwin (1881) reported that when earthworms were offered paper triangles, they always grasped them by the sharpest corner, usually without any attempt to seize any other corner, and this was confirmed by Hanel (1908), although she also found the conflicting evidence that when leaves of lime trees were cut so as to round off the pointed apex, earthworms still grasped them at this point. The overall general tendency seems to be for the earthworms to grip the pointed tips of leaves. For instance, Darwin (1881) reported that of 227 leaves of various species, 181 had been drawn in by the tips of the leaves and only 26 had been pulled in by the base of the petioles. In some unexplained way, earthworms can discern the best way to drag leaves into their burrows with minimum effort, i.e., development of a behavioral pattern. Darwin also described other such patterns shown by individuals of this species during their foraging activities. A study by

Clause et al. has found that earthworm's selection of seeds for consumption may depend more on chemical properties than morphological features of the seed (Clause et al., 2017).

4.5.2 Earthworm Learning

Many workers have shown that earthworms can learn by experience, usually by giving individuals a choice of two courses of action, one of which results in the earthworm receiving an unpleasant stimulus. Such experiments usually use a form of T-maze, with the bottom of the T' as the entrance, and the left- and right-hand arms of the cross-piece providing alternative routes, controlled by stimuli involving either electrodes or a light source in one arm of the "T," to produce negative or positive responses. The first worker to use this type of apparatus to investigate the ability of earthworms to learn by experience was Yerkes (1912). He used a T-shaped glass box, open at the bottom, resting on a plate glass base covered with damp blotting paper. The entrance to the bottom arm of the T-maze was joined to a wooden block through which passed a hole of diameter 14 mm, lined with blotting paper. The earthworms, which were individuals of the species *E. fetida*, were introduced to the maze through this hole. Just inside the entrance to one sidearm, there was a strip of sandpaper on the glass plate and just beyond, two electrodes, resting on a strip of rubber. (In a previous experiment, he used a strip of blotting paper soaked in a strong salt solution instead of the electrodes.) On reaching the junction of the two arms of the crosspiece, the introduced earthworms could turn either into the arm containing the electrodes which was open at the end or into the opposite arm, at the far end of which was placed another hollow wooden block, similar to that at the entrance to the T-maze.

On being introduced to the maze, the earthworms showed no avoidance symptoms, until they entered the arm containing the sandpaper and electrodes. After repeated trials, they learned to avoid contact with the electrodes, and eventually also the sandpaper strip (which acted as a warning of the electrical stimulus), by turning into the opposite arm of the maze. Yerkes also reported that even if up to five anterior segments (including the cerebral ganglia) were removed from individuals, they still retained the imprinted lesson, but only until the cerebral ganglia were regenerated; thereafter, it was lost. Heck (1920) also conducted experiments using a similar type of T-maze, and both Yerkes and he concluded that the earthworms learned to turn into the arm which did not contain shock-producing electrodes, as a direct consequence of avoidance of the learned negative stimulus in the arm containing the electrodes.

Robinson (1953) tested the reactions of *L. terrestris* in a similar apparatus. He found that the behavior of the earthworms in his maze differed from that observed by Yerkes. Before reaching the electrode area, they showed avoidance symptoms to other more generalized stimuli, such as making contact with the walls of the maze. He concluded that Yerkes had oversimplified the nervous reactions of earthworms to

stimuli and that the process of learning to avoid adverse stimuli was more complex. However, Schmidt (1955) compared the behavior of both species under the same experimental conditions (in a maze similar to that of Yerkes and Heck) and observed that individuals of *E. fetida* behaved exactly as Yerkes had seen, and individuals of *L. terrestris* behaved as in Robinson's experiments.

Thus, individuals of the species *L. terrestris* tended to use the entire choice point of the maze as a source of discriminatory cues, whereas *E. fetida* seemed to discriminate mainly on the basis of the sandpaper stimulus. Perhaps such reactions relate to the different habits of the two species. *Lumbricus terrestris* has to seek out its food, whereas *E. fetida* lives in manure or other media rich in organic matter and has food readily available. Perhaps increased sensitivity to stimuli has adaptive value for *L. terrestris* but not for *E. fetida*.

Certainly, the behavioral pattern and the degree of ability to learn to avoid an unpleasant stimulus differ with species, and the behavior of one earthworm species cannot necessarily be used to predict that of another. For this reason, it is unfortunate that different workers have used various species in their experiments. The species tested have included *A. tuberculata* (Heck, 1920; Swartz, 1929), *Bimastos parvus* (Swartz, 1929), *A. longa* (Fraser, 1958), *A. chlorotica*, *L. castaneus* (Heck, 1920), and *L. rubellus* and *Pheretima communissima* (Iwahara & Fujita, 1965).

Several other workers (Swartz, 1929; Lauer, 1929; Bharucha-Reid, 1956) used mazes to study the behavioral patterns of earthworms. Lauer (1929) placed electrodes in both arms of a maze, so that the direction of stimulus could be reversed as required. Krivanek (1956) conditioned batches of individuals of *L. terrestris* to avoid high- and low-intensity light sources, electrical contacts, and tactile stimuli. The conditioned state of earthworms exposed to the high-intensity light source was retained for a further period of 48–72 hours after 42 exposures to the stimulus. This was up to three times as long as that of those earthworms conditioned to react to the low-intensity light source. The conditioned state of earthworms in the batches exposed to electrical shock and tactile stimuli was retained for a period similar to that of those exposed to low-intensity illumination.

Arbit (1957) used electrodes in a T-type maze to examine the behavior and learning response of two batches of individuals of *L. terrestris* in relation to their diurnal cycle of activity. One batch was tested in the maze between 8 p.m. and midnight and the other between 8 a.m. and noon. He found that the evening batch needed significantly fewer attempts before they learned to avoid the stimulus than the morning batch and also that the amount of stimulus needed to start the earthworms moving in the maze (a camel-hair brush, and shining a light) was significantly less in the evening batch than in the morning one. He concluded that generalizations on learned behavioral patterns are not valid from one species of earthworm to another and that the time of day when the pattern is learned relative to the diurnal cycle is also important. Therefore, it seems probable that the ability of an earthworm to acquire a learned response to a stimulus depends, at least partly, on its normal activity at the time of learning (Baldwin (1917) showed that *L. terrestris* is most active between 6 p.m. and midnight.).

The considerable variations in behavioral results have doubtless been due to lack of standardization of experiments in terms of species, age, length of time between tests, treatment of earthworms between tests, time of day for the test, amount of light or dark, design of the maze, and number of trials. Last, and most important, is the need for cleaning of test mazes between tests; earthworms leave mucus trails which they may follow or avoid. Datta (1962) stressed the importance of washing the walls as well as the floor of the maze between trials, and Ressler et al. (1968) suggested that T-maze learning results could be accounted for by unlearned responses to mucus traces, but they did not test this hypothesis. Rosenkoetter and Boice (1975) believed that at least some of the learning phenomena could be accounted for in this way. Nevertheless, there seems to be sufficient evidence to conclude that at least some of the behavior of some species of earthworms can be accounted for by a potential for learning. Much more work is still required on differences between species, neural mechanisms, and behavior in choice situations other than those presented by T-mazes (Howell, 1974). However, even after this considerable body of evidence, Rosenkoetter and Boice (1973) cast some doubt on the theory of T-maze learning by earthworms, attributing their reactions in the reported experiments to either attraction or repulsion by earthworm trails from earlier experiments, but this seems unlikely.

4.5.3 Migrations

A phenomenon that occurs occasionally is that of mass migration of earthworms for some considerable distances on the soil surface. Doeksen (1967) reported a number of instances of this in the Netherlands. Individuals of *E. fetida*, which were living in the soil in greenhouses, migrated in large numbers up the sides of buildings and even onto roofs, during damp, wet, foggy weather. After heavy rain, individuals of the same species living in a dung heap migrated to a nearby farmhouse, climbed up the walls onto the roof, and were even found inside the building. The suggested cause of these migrations was that hydrogen sulfide was produced in the burrows, resulting from anaerobic conditions developing because of poor soil ventilation. Gates (1961) described individuals of species of *Eutyphoeus* and *Lampito* that were seen wandering on the soil surface in daylight after rain in Burma and that *Perionyx excavatus* and some species of *Dichogaster* were found in trees and on the roofs of high buildings. Mass migrations of *Perionyx* species were also reported by the same author. Reddy (1980) reported mass migrations of *Amynthas alexandri*, probably in response to temperature changes.

Large numbers of deep-burrowing species of earthworms commonly appear on the surface of soil after rain, and many of these die, probably due to exposure to ultraviolet light or radiation. Various explanations of this behavior have yet been offered, including low oxygen tensions or chemicals in soil solution that may cause it. We have no evidence as to whether they return to their burrows if they survive.

4.5.4 Luminescence

Phosphorescence or luminescence has been reported to be produced by some species of earthworms. This may show as luminescent blotches or spots on the body, or as a luminous trail behind the earthworm. It is believed that the luminescence is due to a luminous slime exuded from the anus or prostomium, but an alternative suggestion is that it is due to coelomocytes in the protective slime. The function of the luminescence may be protective because it occurs usually when the earthworm is irritated, or in response to vibration or some similar stimulus. Rodionova et al. managed to describe the mechanisms and components which contribute to many species' bioluminescence. For example, *Fridericia heliota's* bioluminescent reactions require luciferase, luciferin, ATP, magnesium ion, and oxygen along with more than a dozen analogues isolated from worm biomass (Rodionova et al).

4.5.5 Diurnal Rhythms of Activity

It is usually assumed that earthworms have diurnal rhythms of activity in response to ultraviolet light and other environmental factors (Ralph, 1957), and experiments where earthworms were kept in continual dark showed that they still maintained a diurnal pattern of activity for up to 7 days after all light stimuli had been removed (Edwards & Lofty, 1977). *Millsonia anomala* was also reported to have a marked pattern of diurnal activity, coming to the surface and casting at between midnight and 9 a.m. in moist soil (Lavelle, 1974). There is evidence of a diurnal rhythm of respiration, with maximal rates occurring at about 6 a.m. and 7 p.m. in Europe (Ralph, 1957; Doekson & Couperus, 1968).

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